

# The breeding biology of Red-Whiskered Bulbul (*Pycnonotus jocosus*) in Xishuangbanna, southwest China

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## ABSTRACT

To fill the gap in breeding biology information about the Red-Whiskered Bulbul (*Pycnonotus jocosus*), in 2013, we studied the breeding biology of this species in Xishuangbanna, southwest China. The breeding began from February and continued until early August. The breeding strategy of *P. jocosus* was more flexible and their nests were only built in cultivated landscapes, whereas, no nest building in native tropical rain forest was found. Small open cup nests were built on 50 different plant species, and at heights ranging from  $2.1 \pm 0.6$  m above the ground ( $n=102$ ). The mean clutch size was  $2.53 \pm 0.51$  eggs ( $n=40$ ) and the mean egg mass was  $2.81 \pm 0.25$  g ( $n=60$ ). The average incubation period was  $11.1 \pm 0.5$  days ( $n=14$ ), and the average nestling period was  $11.0 \pm 0.8$  days ( $n=31$ ). The overall nest success was 34.22%. The hatching and fledging showed either asynchrony or synchrony. Invertebrate food decreased with nestling age, whereas, plant food increased with nestling age. Moreover, distinct parental roles of the parents in nestling period were found. Compared with other passerine species, *P. jocosus* spent less time in incubating (58%). The clutch size, incubation and nestling period of the *P. jocosus* in southwest China were different from those of the *P. jocosus* in India.

**Keywords:** Red-Whiskered Bulbul; Breeding biology; Incubation; Nestling; Parental roles

## INTRODUCTION

The Red-Whiskered Bulbul (*Pycnonotus jocosus*) is a small passerine in the *Pycnonotidae* family, distributed in India, Southeast Asia and South China (Mark, 2009). In South China

it ranges from Southeast Tibet to South Yunnan (MacKinnon & Phillipp, 2011). It inhabits wooded habitats, secondary forests, urban areas, parks, and gardens (Fishpool & Tobias, 2005; Mark, 2009), commonly close to human populations.

*P. jocosus* mainly eats fruits and seeds, and smaller amounts of invertebrates (Yang et al, 2004). It is one of the most common and important seed dispersal agents in anthropogenic open habitats in tropical Asia (Corlett, 1998). However, so far, its breeding biology is quite limited (Appendix 1, available online) (Chidkrua, 1999; Liu, 1992). The information regarding its incubation, parental roles, and nestling food are still lacking. The previous study found the different nesting ecology in the *P. jocosus* inhabiting downtown or periphery of India (Mazumdar & Kumar, 2007), suggesting the flexible breeding strategy of this species.

In this study, we presented details of the breeding biology of *P. jocosus* in Xishuangbanna, including the duration of the breeding season, nest morphology, nest site, clutch size, egg mass, incubation rhythm, length of incubation and nestling periods, parental roles, nestling food, feeding frequency, nestling development, and nesting success. We aimed to collect basic information about its breeding biology in this area, and explore possible reasons for its high abundance in human-dominated environment from its breeding ecology characters.

## MATERIALS AND METHODS

### Study area

The study was conducted in Xishuangbanna Tropical Botanical

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Garden (XTBG, centered at N21°41', E101°25', 570 m a.s.l.), which lies in central Xishuangbanna, southwest China. The dry and wet seasons span from November to April and from May to October, respectively (Zhang & Cao, 1995). In 2013, XTBG experienced an average monthly temperature of 22.1 °C and average monthly precipitation of 139.9 mm (Appendix 2, available online). XTBG is 11.25 km<sup>2</sup> in area, within which 2.5 km<sup>2</sup> is native tropical rain forest, and the remainder is largely cultivated landscapes.

### Nest searching and monitoring

The study was conducted in 2013 from the middle of February (before breeding) to the middle of August (until no newly built nests were found). During this period, nest surveys were conducted every day by an experienced field assistant. Nests were found at different stages (nest building, egg laying, incubation period, or nestling period). Once a nest was located, the following data were collected: nest characteristics (size, height above the ground, and nesting plant species), egg laying date, clutch size, egg mass, incubation rhythm, hatching date, the number of hatchlings, fledging date, and the number of fledglings.

If the nest was found during the egg laying stage, clutch size was recorded by counting the number of eggs every day until no more eggs were laid. Nests that were found during the incubation period weren't included in the clutch size calculation, because some eggs may have been lost before nest discovery. Egg mass was weighed to 0.01 g before incubation started (Ohaus SPS202F pocket scale, Ohaus Corp). Nestling mass was weighed every day at 0800h-0830h from day 0 (the first day that the egg hatched) to day 8 or day 9. Beyond day 9, perturbations to the nest may cause fledglings to leave prematurely. In order to decrease the risk of predation due to our visits, rubber gloves were worn when weighing the nestlings (Whelan et al, 1995).

The feeding visits and fledging behaviors of 16 broods were observed by using video recorders (SONY HDR-PJ760E). Other broods were checked once daily. The feeding visits were recorded from the day that the first egg hatched until the last nestling fledged or the nests failed. Recordings started between 0800-0900h, and ended between 1700h-1800h. Cameras were set up at a distance of 1-4 m away from the nest, pointing down at an angle of approximately 30° (Smith & Montgomerie, 1991). The parents usually fed nestlings within a few minutes of camera set-up and recording; the camera did not interfere with nest activity.

### Incubation

The incubation period was the time between the last egg laid and the first egg hatched (Auer et al, 2007). We used temperature data loggers (Model Lu Ge L91) to monitor the onset of incubation and incubation rhythm (Badyaev et al, 2003; Cooper & Mills, 2005; Hartman & Oring, 2006). Some broods initiated incubation at the end of egg-laying and all the young were then hatched together, which is defined as "hatching synchrony". Others began incubation before all the eggs were laid, thus some young were hatched before the others, often on

successive days, which is termed as "hatching asynchrony" (Clark & Wilson, 1981). A sudden increase or decrease in temperature indicates the arrival or departure of the parents. This assumption was verified by comparing videotape recordings and temperature logger data collected at one nest, observing high concordance between the two data types. The data loggers were installed as far as possible before clutch completion to determine the onset of incubation. One of the probes was placed in nests lightly covered with existing nest materials, and another probe was placed outside of the nest (Hartman & Oring, 2006). The temperature was recorded once each minute.

We evaluated the following variables characterizing incubation behavior from the data logger recordings: the onset of incubation, and night resting period (the time between the last evening arrival and the first morning departure from nest). The daily active period was the length of time remaining after the night resting period. We then calculated the mean on-bout duration (mean time for each incubation bout) and mean off-bout duration (mean time interval between two continues incubation) (Balakrishnan, 2010; Kovařík et al, 2009).

### Feeding frequency, nestling food and parental roles

The nestling period was defined as the time between the first egg hatching to the last member of the brood fledging (Temba et al, 2014). Feeding frequency was defined as the number of feeding visits each hour and the number of visits without food was not used to calculate feeding frequency. Food was divided into two categories: invertebrate or plant food, which could be clearly identified from video recordings. We used feeding volume to compare invertebrate and plant food composition in the nestlings' diet, which was more precise than feeding frequency. Food volume was scored by comparing the item volume to the volume of parents' bill, and divided into four classes: 0.25, 1, 1.75, and 2.5 bill-equivalents (Dearborn, 1998). The contributions of invertebrate and plant food were compared as below:

$$IP=IV/FV \quad (1)$$

$$PP=PV/FV \quad (2)$$

In which, IP represents the percentage of invertebrate food, IV represents the total volume of invertebrate food provided by each parent during the nestling period, FV represents the total food volume provided by each parent during the nestling period, PP represents the percentage of plant food, PV represents the total volume of plant food provided by each parent during the nestling period.

Male and female *P. jocosus* are usually difficult to distinguish due to an absence of marked sexual dimorphism. However, we found that in two nests the adult birds have different color patterns on their faces (Appendix 3, available online). Although the male and female still could not be distinguished, it offered the possibility to analyze whether the male and female adults contributed equally to nestlings in brooding nestlings after feeding visits, feeding frequency, contribution of invertebrate and plant food (Adler & Ritchison, 2011), time spent at the nest (including the time spend on brooding nestlings and feeding visits), and fecal sac clearing (the number of feces cleaned by every parent in the nestling period) (Dell'Omo et al, 1998).

### Breeding success

A nest was considered failed if there were the following occurrences: egg loss during the incubation period, broken eggs, cold eggs, no hatchling emergence even when the incubation time had exceeded the maximum for other observations, and signs of predation (i.e., disturbed nests with the nestlings disappearing before fledging, nestlings that died in the nest with wounds produced by parasites, or nestlings found on the ground with nests upturned after a rainstorm).

Successful nests were defined as those where at least one nestling fledged. Hatching success was defined as the total number of hatchlings from the total number of eggs, fledging success as the total number of fledglings from the total number of hatchlings, and nesting success as the total number of fledglings from the total number of eggs (Buij et al, 2013; Bensouilah et al, 2014).

### Data analysis

ANOVA was used to calculate whether feeding frequency and invertebrate composition changed with age. For plant food, nonparametric tests (Kruskal-Wallis rank sum test) were used, as the variances did not exhibit homoscedasticity. Nestling growth rate constant ( $k$ ) and asymptote mass ( $A$ ) were calculated using a logistic growth equation  $y = A / (1 + e^{-(k \cdot (t - t_i))})$  (Ricklefs, 1976), where  $t_i$  is the inflection point of the growth curve. All of the mean values are reported with the standard deviation (mean $\pm$ SD).

## RESULTS

We found 102 nests from February to August in 2013. Among them, 40 nests were found at the egg laying period, 47 were found at the incubation period, and 15 were found at the nestling period. *P. jocosus* laid eggs from February to July and the breeding season ended in early August. The breeding peak lasted from April to June (Figure 1).

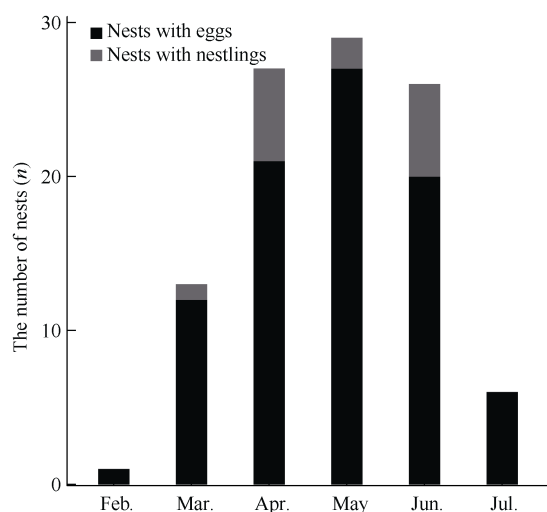


Figure 1 Nesting season of *P. jocosus* at XTBG, 2013

### Nest placement and measurement

All nests were built in cultivated landscapes. Nests were found in 50 different plant species. Ten nests were found on the *Areca catechu*, which was the most frequently used nesting plant species. Nest height was  $2.1 \pm 0.6$  m above ground ( $n=102$ , range=0.9-3.8 m). Nests were shallow and bowl-shaped, built of thin grass leaves, fine roots, and spider silk outside of the nest. The inside diameter of nests was  $6.5 \pm 0.7$  cm ( $n=75$ , range=4.5-9.0 cm), outside diameter was  $9.1 \pm 1.2$  cm ( $n=75$ , range=6.9-14.5 cm), inside depth was  $4.8 \pm 0.7$  cm ( $n=75$ , range=3.3-7.0 cm), and outside height was  $6.6 \pm 1.0$  cm ( $n=75$ , range=4.5-8.6 cm).

### Clutch size and egg mass

Eggs were oval in shape, and had a pale-white base color with dense pink speckles towards the broad end (Figure 2). Females laid eggs on consecutive days and one egg per day. The mean clutch size was  $2.53 \pm 0.51$ , mostly ranging from 2-3 eggs ( $n=40$ ), however, one nest had four nestlings when discovered. Egg mass was  $2.81 \pm 0.25$  g ( $n=60$ , range=2.24-3.59 g).



Figure 2 Eggs and nest of the *P. jocosus*

### Incubation

The mean incubation period was  $11.1 \pm 0.5$  days ( $n=14$ , range=10-11 days). From video recording we found that only one adult incubated the eggs ( $n=2$ ). *P. jocosus* incubated continuously over the nights (night nesting period) from 1903h $\pm$ 49 min to 0647h $\pm$ 37 min ( $n=8$ ). The parent spent an average of  $58 \pm 13\%$  of daylight hours on incubating. The average on-bout lasted  $17.0 \pm 9.3$  min ( $n=8$ ). Parents left nests at an average of  $2.9 \pm 1.2$  times/hour., and the average off-bout was  $10.9 \pm 4.0$  min ( $n=8$ ).

Five temperature data loggers were installed prior to clutch completion, thus the onset of incubation could be clearly determined. Two broods were completed before incubation began while the other 3 were incubated before the clutch was completed. The rate of hatching asynchrony and synchrony were 82% and 18%, respectively, in the 50 nests.

### Nestling period, feeding frequency, nestling food and parent roles

The average nestling period was  $11.0 \pm 0.8$  days ( $n=31$ , range=10-13 days). Based on the video observation, the average nest feeding frequency was  $7.5 \pm 3.5$  times/hour ( $n=20$ ), and the feeding frequency differed among nestling ages,

gradually increasing until hitting a peak at day 8 (ANOVA  $F_{12, 124}=3.37$ ,  $P<0.01$ ; Figure 3).

Both invertebrate and plant food were provided to nestlings, but invertebrates significantly declined with nestling age (ANOVA  $F_{12, 119}=8.26$ ,  $P<0.001$ ), while plant food significantly increased with nestling age (nonparametric tests  $\chi^2=80.12$ ,  $df=12$ ,  $P<0.001$ ) (Figure 4).

From the two nests where the parents could be distinguished, we found that parents have different parental roles over the nestling period (Table 1). Both parents fed nestlings and cleaned feces by consumption or removal. However, only one parent would brood nestlings after feeding. We defined the parent who

brooded nestlings as A, and the other as B. Parents A and B were different in feeding frequency. During the whole nestling period, parents A and B finished  $31.04\pm16.25\%$  and  $65.04\pm18.93\%$  feeding visits, respectively. In 4.75% of the 2 190 feeding visits, the two parents could not be distinguished. The contributions in food provision, especially in invertebrates were different in parent A and B. Parent A spent more time on brooding nestlings and feeding visits during the nestling period (average feeding visit of Nest I: parent A:  $71\pm46$  s, parent B:  $37\pm21$  s; Nest II: parent A:  $114\pm24$  s, parent B:  $37\pm16$  s) (Figure 5). The feces cleaning effort in parent A was lower than parent B. Nest II had only one nestling at day 7, as one of them died from parasite attack.

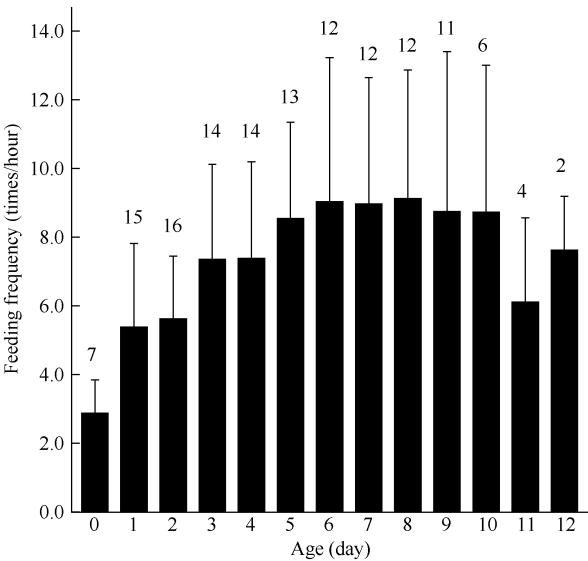


Figure 3 Relationship between feeding frequency and nestling ages for *P. jocosus* nestling birds at XTBG, 2013  
Numbers above error bar are sample size (*n*); Day 0 is the day the first nestling was hatched.

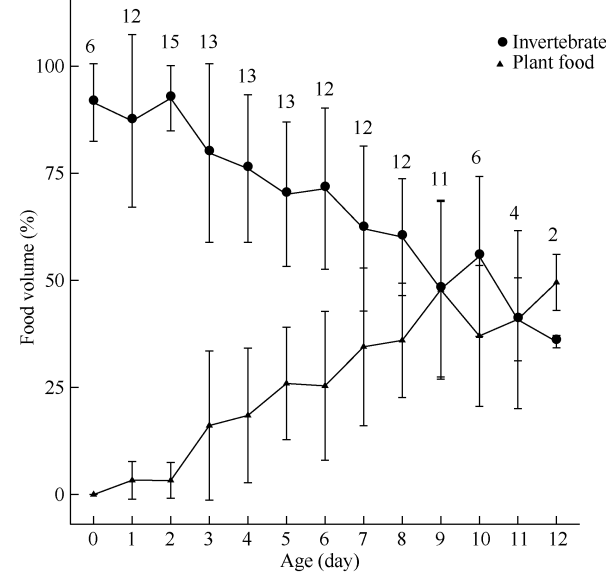


Figure 4 Age-related invertebrate and plant food volume percentage (mean±SD) change of *P. jocosus* at XTBG, 2013  
Numbers above error bar are sample size (*n*); Day 0 is the day the first nestling was hatched.

Table 1 Relative contributions of parent A and B during the nestling period in XTBG, 2013

Nest	Brood size	Parents	Feeding frequency (times/hour)	Invertebrate food (%) <sup>a</sup>	Plant food (%) <sup>a</sup>	Feces cleaning effort <sup>b</sup>	Brood nestling
I	3	A	2.53	11.14	14.48	90	Yes
		B	3.80	47.90	22.57	203	No
II	2	A	1.53	17.39	3.39	56	Yes
		B	2.95	56.94	17.39	167	No

<sup>a</sup>: Food type of 3.91% and 4.89% of the food volume from nest I and II could not be distinguished, respectively; <sup>b</sup>: Feces cleaning efforts are defined as the number of feces consumed or transported by adult birds over the nestling period.

### Nestling development

Nestling mass growth exhibits an “S” curve (Figure 6), with a good fit for the logistic growth equation. The growth rate constant (*k*) was 0.45, and the asymptote (*A*) was 18.10 g.

### Nest leaving

Eleven of 46 broods were recorded by video, the nestlings of most broods (*n*=44) fledged on the same day (synchrony). Only

two broods fledged asynchronously (fledged over three days). In these cases, after the older offspring fledged, the parents continued to feed the remaining nestlings until they fledged. The rate of fledging synchrony and asynchrony were 95.65% and 4.35%, respectively (*n*=46).

### Nest success

For a total of 225 eggs (*n*=87 nests) laid, hatching success

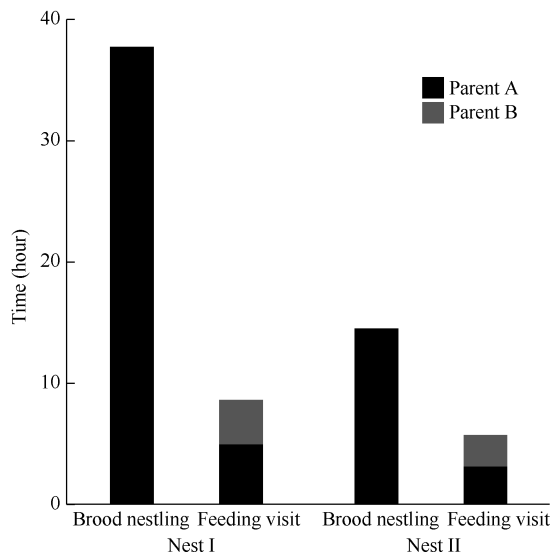


Figure 5 Time spent at the nest of parent A and B of *P. jocosus* during nestling period at XTBG, 2013 (Video recording time: nest I: 100.46 hours; nest II: 96.99 hours)

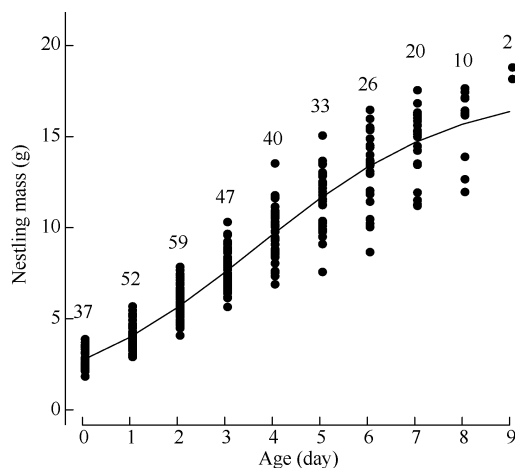


Figure 6 Individual mass growth of *P. jocosus* nestling at XTBG, 2013

Day 0 is the day the first nestling was hatched; The logistic function was  $y=18.10/(1+e^{(-0.45*(t-4.10)})}$ ,  $r^2=0.85$ ; Numbers above black dot are sample size ( $n$ ).

Table 2 Nest ( $n=87$ ) failure factors of *P. jocosus* in XTBG, 2013

Stages	Reasons	Number of eggs or nestlings lost ( $n$ )	Percentage (%)
Eggs	Infertile	12	11.54
	Predation	65	62.5
	Desertion	24	23.08
	Strom	3	2.88
Nestlings	predation	30	68.18
	Parasite	12	27.27
	Storm	2	4.55

was 53.78% ( $n=50$  nests) while fledging success was 63.63% ( $n=34$  nests), and overall nest success was 34.22%. The average number of fledglings per successful nest was  $2.26 \pm 0.67$  ( $n=34$  nests, range=1-3).

#### Nest failure

Many factors contributed to nest failure (Table 2). Eggs failed due to infertility, storms, parent desertion, and predation; nestlings died from nest parasites (larvae of an unknown dipteran species), storms, and predation. Storms are a threat to the nests of *P. jocosus* as they are shabby and are not robust to bad weather. Reasons for nest desertion during the incubation period are unknown.

Predators are the main factor resulting in nest failure (Table 2, eggs stages: 62.5%, nestlings stages: 68.18%), however direct observations of predators were limited and mainly included one Himalayan striped squirrel (*Tamiops macclellandi*) which predated a nestling, and one tree shrew (*Tupaia sp.*) which predated a nestling. One squirrel (*Sciuridae sp.*) was also observed attacking a new fledgling.

#### DISCUSSION

In this study, we obtained basic breeding biology information about the nest, clutch size, incubation, feeding frequency, nesting success, parental roles, and nestling food of *P. jocosus* in Xishuangbanna. All nests were observed in cultivated landscape. *P. jocosus* can use large numbers of plant species as nest building sites, indicating that they can adapt to human-dominated habitats.

#### Nests

*P. jocosus* were only observed building nests in cultivated landscape. Nests were built in wide range of plant species, compared to research on *Pycnonotus sinensis*, which built nests in 11 plant species ( $n=99$  nests) (Lan et al, 2013), and some other open-cup passerine species such as *Sporophila caerulea*, which built nests in 8 plant species ( $n=41$  nests) (Francisco, 2006) and *Garrulax henrici* which built nests in 13 plant species ( $n=91$  nests; Lu et al, 2008), *P. jocosus* has plasticity with respect to nesting plant species.

#### Incubation and nest leaving

Similar to most bulbul species (Fishpool & Tobias, 2005), only one parent performed incubation in our population. Parent *P. jocosus* only spent  $58 \pm 13\%$  of daylight hours to incubate, less

than the incubation time of some passerine species such as *Junco phaeonotus* (76.9%) (Weathers & Sullivan, 1989), *Dendroica caerulescens* (64%) (Joyce et al, 2001), and *Anthus pratensis* (77.19%) (Kovářík et al, 2009). The shorter incubation time may result from the high ambient temperature, as the mean temperature was 28.07 °C (range: 17.3 °C–45.9 °C) during 0700–1900h in our study site. Previous research suggests that below 26 °C chicken embryos will suspend development (Conway & Martin, 2000). Temperature fluctuations within an appropriate range during incubation would increase hatching success (Sun, 2001). The embryo would not die from exposure when the parent left the nest in high ambient temperature, and it would benefit *P. jocosus* by permitting the parent to spend less time on incubation and more time on foraging in the study site.

Although previous study reported that *P. jocosus* begins incubating immediately after the first egg was laid (Fishpool & Tobias, 2005), in our study, the incubation was initiated either before or after the clutch was completed. The high asynchrony (82%) of hatching indicates that the incubation of most of the broods was initiated before the clutch was completed. However, except two broods (4.35%), most of the broods fledged on the same day (95.65%). The low asynchrony in fledging than that in hatching is in accordance with previous study (Viñuela & Bustamante, 1992). Hatching synchrony is considered to be favorable, because the nestlings may be more easily cared when they are fledged (Lack, 1954, 1968). On the other hand, asynchronous birth can also be adaptive under some conditions (Podlas & Richner, 2013). Previous studies indicate that asynchronous hatching could reduce the competition between chicks and energy wasted by begging offspring, and also decrease the reproductive loss to parents (Cotton et al, 1999; Mainwaring et al, 2012). Thus parents may use a brood reduction strategy in unpredictable environments. If predation risks or inadequate food resources restrict the feeding behavior, parents may prefer older nestlings and starve younger ones to reduce overall reproductive losses (Lack, 1954; Morandini & Ferrer, 2015; Williams et al, 1993). In the two broods that fledged asynchronously, the older chicks fledged earlier and received more food, but there was no difference between the nestlings in broods that fledged synchronously (Li, unpublished data).

#### Clutch size, incubation period and nestling period

The clutch size of most African and Asian bulbuls is usually 2–3 eggs, but some species also lay 4–5 eggs (Kitowski, 2011). The clutch size of *P. jocosus* in Xishuangbanna was similar, but the mean clutch size was smaller than *P. jocosus* in India (Mazumdar & Kumar, 2007). The differences in clutch size could be influenced by parent's feeding ability, predation pressure, and food resource abundance (Lack, 1954; Eggers et al, 2006). The nesting success (34.22%) in our population was lower than that in India (city center: 72.2%; city outskirts: 80.5%), and predation was a major reason of nest failure (eggs stages: 62.5%, nestlings stages: 68.18%) (Table 2). Therefore, we assume that high predation pressure was the major reason of the small clutch size in our population. The incubation and

nestling period of *P. jocosus* were also shorter than that in India (Mazumdar & Kumar, 2007). Previous study suggests that increased nest predation risk favors a shorter nestling period (Martin, 1995), thus, the short nestling period in our population may be the result of high predation pressure.

High predation pressure limits food provision, restrains nestling development, and prolongs nestling period (Martin, 1992, 1995; Ricklefs, 1976), whereas, long nestling period may increase the risk of being predated. Thus, a smaller clutch size resolves this contradiction (Martin, 1992, 1995).

#### Nest success

Predation was the major factor limiting the hatching and fledging success in our study. The total nest success of *P. jocosus* in our population was lower than that in India (Mazumdar & Kumar, 2007), but higher than other *Pycnonotus* species (Kitowski, 2011; Rao et al, 2013). In our study site, the level of nest success was similar to the Chinese Bulbul (*Pycnonotus sinensis*; Lan et al, 2013).

Although the observed signs were consistent with predation in a large number of nests, little is known about the nest predators. We recorded that one Himalayan striped squirrel was predated a nestling, and one squirrel was attacking a fledgling. Potential predators in our study area included but were not limited to: squirrels, stray cats and predatory birds (*Buteo buteo*, *Spilornis cheela*, *Pernis ptilorhynchus*, *Centropus sinensis*, *Urocissa erythrorhyncha*, and *Accipiter trivirgatus* are common in our study site). Another study carried out at the same study location reported that snakes (*Oligodon cyclurus*) were also nest predators (Quan & Li, 2015).

#### Breeding season and nesting cycle

The breeding season in our study area was 1–2 months later than that in Changwat Loei of Thailand (Chidkrua, 1999). The breeding season may start earlier in lower latitudes (Conover & Present, 1990), and the latitude of our area was higher than Thailand. The peak of the egg laying period matched the peak of temperature, but was offset from the peak of precipitation. *P. jocosus* spends 5–7 days to construct the nest (Mazumdar & Kumar, 2007). The female lays eggs in 2–3 days. The sum of incubation period and nestling period was about 22 days. Fledglings still required parental care for 34 days (Fishpool & Tobias, 2005). Given the long breeding season (Feb.–Aug.), it seems that adults have time for producing more than one brood each breeding season.

#### Parental roles

Differences in parental roles between the sexes in the nestling period are a common phenomenon in passerines (Neudorf et al, 2013). However, little information about parental roles has been reported for bulbuls. From our observations of individually recognizable birds in this monomorphic species, we observed that *P. jocosus* had parental roles in incubation and nestling periods. Only one parent incubated the eggs, and the partner might be responsible for guarding. Both males and females provisioned nestlings and cleaned feces, but the tasks were not equally shared. Only one of the adults would incubate nestlings

after feeding visits.

### Nestling food

The parents of *P. jocosus* brooded nestlings and provided more invertebrates when nestlings were younger. As altricial nestlings are poikilotherms, for several days after hatching they need parents to keep them warm (Ricklefs & Hainsworth, 1968; Watson, 2013). The age-related changes in nestling diet might be because that the adults of *P. jocosus* eat more plant foods in their diet (Yang et al, 2004). Or that was a trade-off for parents (Trivers, 1974) as there was a significant positive correlation between invertebrate biomass and faster growth rate in wood thrush (*Hylocichla mustelina*) nestlings (Duguay et al, 2000). The rich proteins in invertebrates promote faster growth, but they are more difficult to obtain than plant food (Morton, 1973). As the food demanding increases with nestling age, the parents might not be able to find enough invertebrates alone.

These obvious variances indicate that *P. jocosus* is highly flexible in their breeding strategies. As their nests can be easily found and accessed, we suggest that *P. jocosus* could be regarded as a model species in future studies of Asian bird nesting ecology.

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